

General morphology of the oral cavity of the Nile crocodile, *Crocodylus niloticus* (Laurenti, 1768). I. Palate and gingivae

J.F. PUTTERILL^{1*} and J.T. SOLEY²

ABSTRACT

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The heads of nine 2.5 to 3-year-old Nile crocodiles (*Crocodylus niloticus*) were obtained from a commercial farm where crocodiles are raised for their skins and meat. The animals from which these specimens originated were clinically healthy at the time they were slaughtered. A detailed description of the macroscopic and microscopic features of the palate and gingivae of the Nile crocodile is presented and the results are compared with published information on this species and other Crocodylia. The histological features are supplemented by information supplied by scanning electron microscopy. Macroscopic features of interest are the small conical process situated at the base of the first two incisors of the maxilla, the distribution of cobbled units on the palate, and the broad dentary shelf forming the rostral aspect of the mandible. Histologically the palate and gingivae did not differ significantly from each other and both regions showed a presence of Pacinian-type corpuscles. Two types of sensory structures (taste receptors and pressure receptors) were identified in the regions examined, both involving modification of the epithelium and the underlying connective tissue.

Keywords: *Crocodylus niloticus*, histology, morphology, Nile crocodile, oral cavity, scanning electron microscopy

INTRODUCTION

The morphology and microscopic anatomy of the reptilian oral cavity has received much attention in the literature (for a review see Luppa 1977), with most studies concentrating on the description and location of glandular tissue, taste receptors and

epithelial specialisation of the region. Attention has also been given to the embryological and evolutionary development of these specialisations. Similarly, most studies on the oral cavity of crocodylians have concentrated on specific morphological features of this region.

Röse (1893) reported the presence of glandular tissue situated in pits between the teeth of the maxilla (*glandulae palatinae*) in *Crocodylus porosus* and described the embryological development of these glands. Woerdeman (1920) reviewed earlier literature (ca. 1888 to 1914) on the subject and emphasised discrepancies amongst the authors regarding the presence or absence of oral glands in Crocodylia. Farenholz (1937) reported two areas in the palate in which glands occur, *viz.*, median palatine

* Author to whom correspondence is to be directed

¹ Electron Microscopy Unit, Onderstepoort Veterinary Institute, Private Bag X05, Onderstepoort, 0110 South Africa. E-mail: john@moon.oivi.ac.za

² Department of Anatomy and Physiology, Faculty of Veterinary Science, University of Pretoria, Private Bag X04, Onderstepoort, 0110 South Africa

glands found only in *Caiman* spp. and small glands at the median aspect of the maxillary teeth, found in *Caiman* spp. and *Alligator mississippiensis*. However, Taguchi (1920) found glandular tissue "in the submucosa of the caudal part of the palate and the oral surface of the velum". Kochva (1978) extensively described glandular tissue in reptiles, but only fleetingly refers to the Crocodylia.

Bath (1905, 1906) described the histology of taste receptors in the oral cavity, pharynx and oesophagus of *Crocodylus niloticus* (*sic.*) and *Alligator mississippiensis* (*sic.*), finding no clear distinction between those seen in these species and those of higher animals. Luppá (1977), who generalised his description of the histological composition of the reptilian oral cavity, stated that "taste buds were scattered throughout the oral epithelium in reptiles and that in *Lacerta* they were most numerous laterally and on the palatal folds." Hulanicka (1913) investigated the innervation of the tongue, palate and the skin of *Crocodylus niloticus* and *Alligator lucius* and described five different nerve endings in the regions studied. *Alligator lucius* represents *A. mississippiensis* (F.W. Huchzermeyer, personal communication 2002).

Fuchs (1908, cited by Barge 1937) postulated the formation of the secondary palate in the Crocodylia and compared this formation to other reptiles, concluding that the secondary palate of crocodiles was unique amongst the reptiles. Barge (1937) described the embryological development and phylogeny of the secondary palate in crocodiles. Ferguson (1979) investigated the developmental mechanisms in normal and abnormal palate formation in the American alligator (*A. mississippiensis*) and concluded that the Crocodylia showed characteristics which were part mammalian and part reptilian, a unique combination which made them a useful model to study palatogenesis.

Dentition in Crocodylia has also received much attention in the literature. Of note is the paper by Poole (1961) who described tooth replacement in *C. niloticus*, the studies by Westergaard & Ferguson (1986, 1987) who described the development of dentition in hatchling and juvenile *A. mississippiensis*, and the article by Kieser, Klapsidis, Law & Marion (1993) who examined heterodonty and patterns of tooth replacement in *C. niloticus*. Edmund (1962, 1969) also made a major contribution to studies on dentition in the Reptilia, including the Crocodylia, describing the sequence and rate of tooth replacement in these reptiles.

Although detailed descriptions of specific components of the crocodylian oral cavity have been presented, only a few studies have reported on the general histological features of this region. Reese (1913) studied the histology of the enteron of the "Florida alligator", which included the oral cavity. Reese's description, however, concerned histological differences between hibernating and feeding, captive animals. Taguchi (1920) compared similar regions of the oral cavity to those examined by Reese (1913) in three species of Crocodylia, namely, *Alligator sinensis*, *Krokodilus porosus* and *Krokodilus vulgaris*. The latter is believed to represent the Nile crocodile, *Crocodylus niloticus* (see <http://www.flmnh.ufl.edu/natsci/herpetology/turtcroclst/chk1st2.htm>). Throughout this paper, and pertaining only to Taguchi (1920), "*Krokodilus*" is referred to as "*Crocodylus*" and "*K. vulgaris*" as "*C. niloticus*". In Chiasson's (1962) publication on the anatomy of the alligator, components of the oral cavity (palate and tongue) are briefly mentioned without any further detail being given. Similarly Parsons & Cameron (1977), who examined the relief of the gastro-intestinal tract of the Reptilia, including the Crocodylia, only start their description from the oesophagus and do not describe the morphology of the oral and pharyngeal cavities.

In view of the paucity of information concerning the general histological features of this part of the upper digestive tract, this paper presents a general topographical description of the oral cavity as well as the macroscopic and microscopic features of the palate and gingivae of the Nile crocodile, *Crocodylus niloticus* (Laurenti, 1768) and compares the results with published information on this species and other Crocodylia. The histological features are supplemented by information supplied by scanning electron microscopy (SEM). Morphological features of the tongue will be presented in another paper.

MATERIALS AND METHODS

Experimental animals

The heads of nine 2.5 to 3-year-old Nile crocodiles were obtained from a commercial farm where crocodiles are raised for their skins and meat. The lengths of the animals sampled ranged from 1.2–1.5 m and they were clinically healthy at the time they were slaughtered. The animals were killed by shooting them in the brain at close range using a .22 calibre rifle. After the carcasses had been skinned and eviscerated the heads were removed

and immersion-fixed in a large volume of 10 % phosphate-buffered formalin in plastic buckets for a minimum period of 48 h. Care was taken to exclude air from the oral cavity by wedging a small block of wood in the angle of the mouth prior to immersion in the fixative. Samples from the palate and gingivae were taken from the heads and processed for light microscopy (LM) and scanning electron microscopy (SEM) according to the procedures detailed below.

Topography

Prior to sampling, all nine heads were utilised for a description of the gross anatomical features and topographical relationships of the structures in the oral cavity. Macrophotographs were recorded digitally using a Nikon Coolpix 995 (Nikon, Tokyo, Japan) digital camera or on 35 mm film using a Chinon X-7 (Chinon, Tokyo, Japan) single lens reflex camera, respectively. The oral cavities of these heads were also examined and micrographed using a stereomicroscope (Wild M-400 Photomakroskop, Heerbrugg, Switzerland) to obtain higher magnification micrographs of specific topographical features.

A dried skull from a 5-year-old (approximate age) specimen was used to confirm the position and naming of teeth in the maxilla and mandible as well as to provide supporting evidence for the anatomical description. Teeth were named and numbered according to Kieser *et al.* (1993).

Light microscopy

Samples of the gingiva from the mandible were removed from the various regions indicated in Fig. 1 and were based on the position of the incisor and canine teeth. The portion of gingiva caudal to the indicated regions, i.e. the region involving the molar teeth, was too firmly attached to the underlying bone to permit suitable samples to be taken. The mucosa of the palate was also sampled according to the dental arrangement of the teeth, i.e. from regions I 1 to I 5, C 1 to C 5 and M 1 to M 8 as shown in Fig. 2. As the gingiva of the maxilla appeared macroscopically to be continuous with the palate, these specimens were removed together with the samples of the palate. A similar set of specimens (adjacent tissue) from all the indicated regions of the mandible and palate was taken at the same time for SEM examination.

Samples for LM were dehydrated through 70, 80, 96 and 2X 100 % ethanol and further processed through 50 : 50 ethanol : xylol, 2X xylol and 2X par-

affin wax (60–120 min per step) using a Shandon model 2LE Automatic Tissue Processor (Shandon, Pittsburgh, PA, USA). Tissue samples were finally embedded manually into paraffin wax in brass moulds. Sections were cut at 4–6 μ m, stained with haematoxylin and eosin (H&E) (Luna 1968) or periodic acid-Schiff (PAS) (Pearse 1985) and viewed and micrographed using a Reichert Polyvar (Reichert, Austria) compound light microscope fitted with a differential interference contrast (DIC) prism.

Scanning electron microscopy

The samples of the gingivae and palate obtained as indicated above and which had been fixed in 10 % phosphate-buffered formalin for a minimum of 48 h were subsequently rinsed for several hours in water to remove traces of phosphate buffer. These samples were routinely dehydrated through an ascending ethanol series (50, 70, 90, 95 and 3X 100%—60 min per step) and critical point dried from 100 % ethanol through liquid-CO₂ in a Polaron Critical Point Drier (Polaron, Watford, England). The samples were then mounted onto brass or aluminium viewing stubs (to expose the epithelial surface) with a conductive paste (carbon dag) and sputter coated with gold using a Balzers 020 Sputter Coater (Balzers Union, Liechtenstein). Specimens were viewed and photographed using a Hitachi S-2500 scanning electron microscope (Hitachi, Tokyo, Japan) operated at 8 kV.

RESULTS

Macroscopic features

The oral cavity had the form of an isosceles triangle (Fig. 1 and 2) and was dorso-ventrally flattened, severely limiting the space within the cavity. The roof of the cavity was formed exclusively by the palate and the indistinct gingiva with which it was continuous. The caudal limit of the roof was demarcated by the notched dorsal component of the gular valve, whereas the rostral limit of the palate was occasionally characterised by the presence of two deep pits which accommodated the first two incisors of the mandible (Fig. 2). Between the two pits (or at the base of the two I 1 teeth) was a small, rigid, conical process (Fig. 2) which emerged from a low-profiled ridge above the anterior palatine foramen. The tip of this process was housed within a shallow depression in the mandible at the base of the first two mandibular incisors (Fig. 1 and 3). The surface of the palate had a cobbled appearance

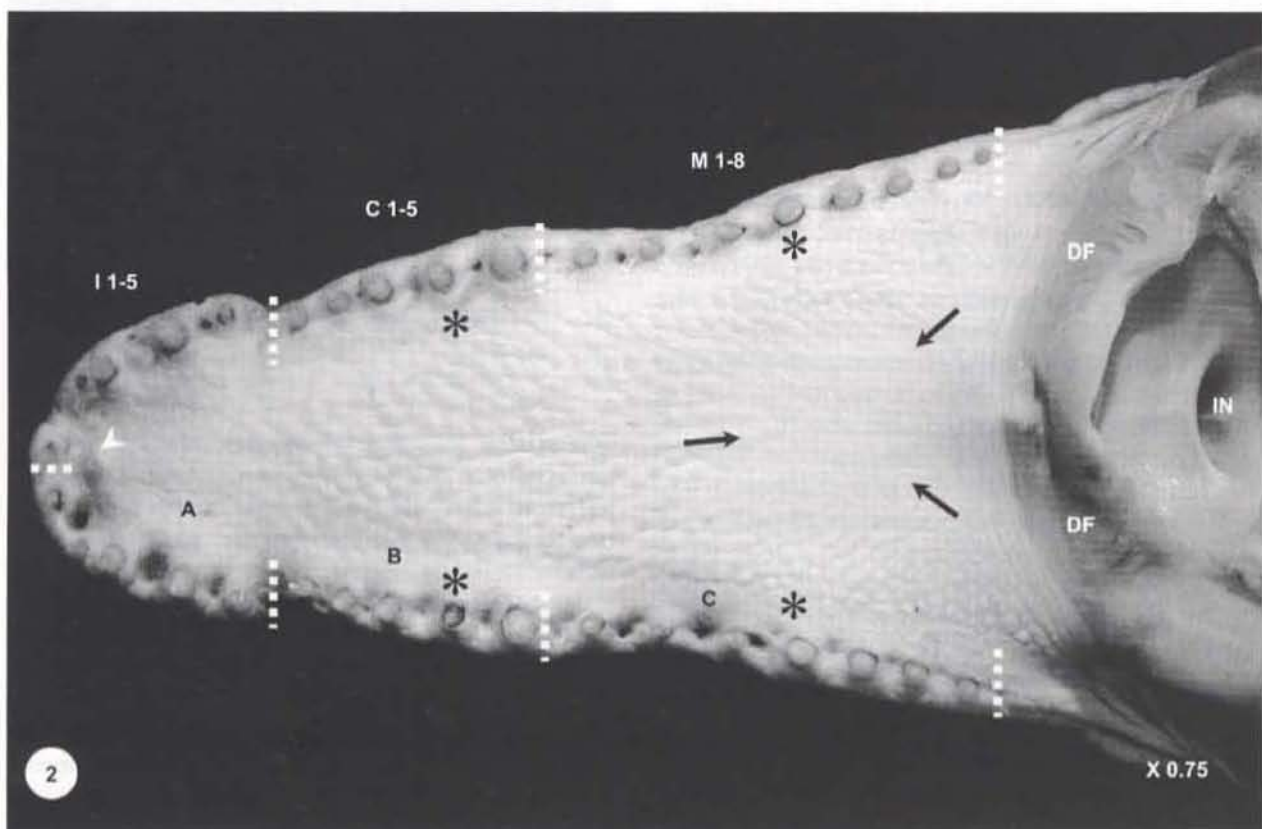
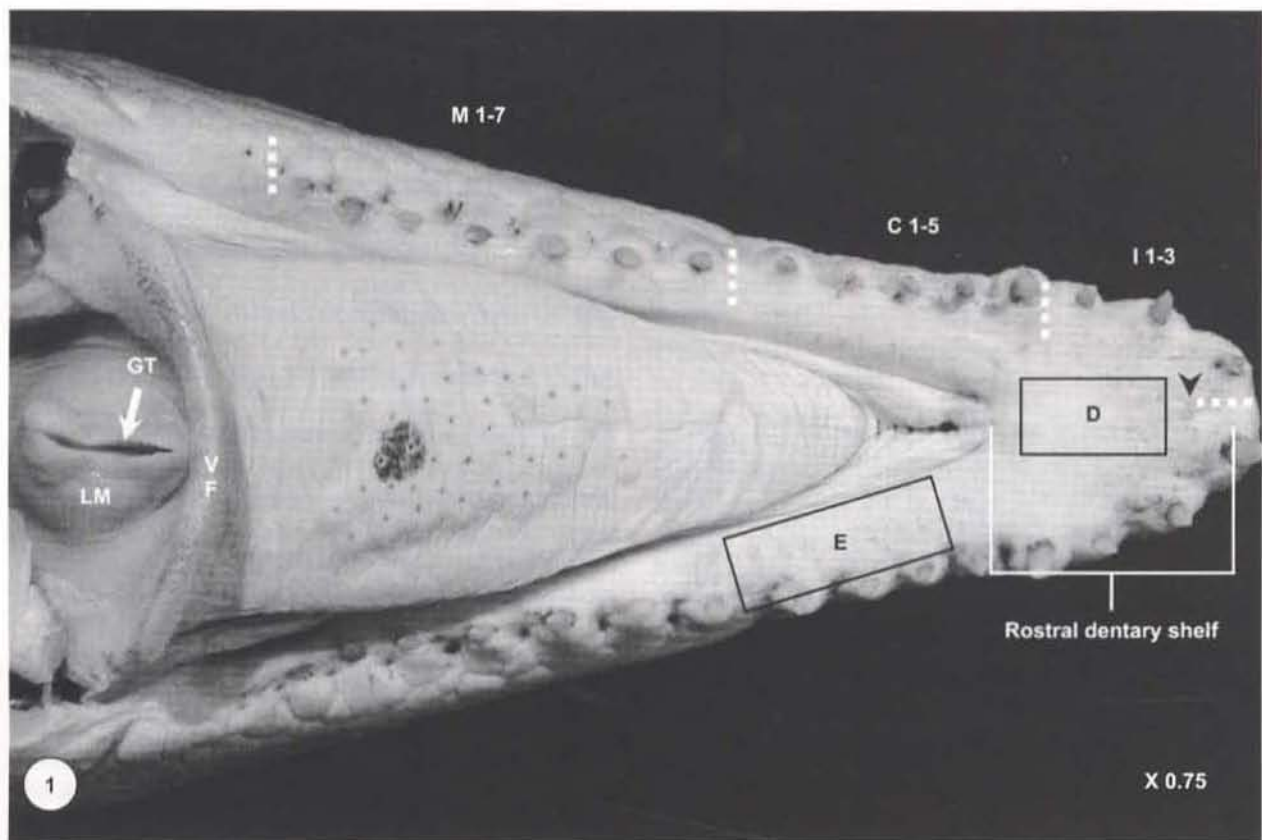


FIG. 1 Macrophotograph of the mandible with the tongue *in situ* showing the dental arrangement of the incisor (I 1–3), canine (C 1–5) and molar (M 1–7) teeth, demarcated by the stippled lines. The sampling sites for histology of the gingivae (D and E) are also indicated. The rostral dentary shelf is indicated in the region above the symphysis of the dentary bones. The black arrowhead indicates the position of the shallow depression which houses the small, rigid, conically formed process, situated at the base of the I 1 teeth, seen in Fig. 2. The glottis (GT) and laryngeal mound (LM) are shown *in situ* on the floor of the pharyngeal cavity and the ventral fold (VF) of the gular valve is seen separating the ventral aspects of the oral and pharyngeal cavities. Formalin fixed specimen. X 0.75

FIG. 2 Macrophotograph of the maxilla and palate showing the dental arrangement of the incisor (I 1–5), canine (C 1–5) and molar (M 1–8) teeth, demarcated by the stippled lines. The smooth area of the palate, demarcated by the black arrows, lies above the left and right posterior palatine foraminae. The small, rigid, conical process, situated at the base of the I 1 teeth, is indicated by the arrowhead. Also note the smooth zone of mucosa forming the gingiva adjacent to the teeth (asterisks) which stretches from approximately I 5 to M 8 on both sides of the maxilla. The common opening of the internal nares (IN) is seen on the roof of the pharyngeal cavity as well as the dorsal fold (DF) of the gular valve which separates the dorsal aspects of the oral and pharyngeal cavities. Samples of the mucosa of the palate and gingiva were removed from regions A, B and C as indicated on the photograph. Formalin fixed specimen. X 0.75

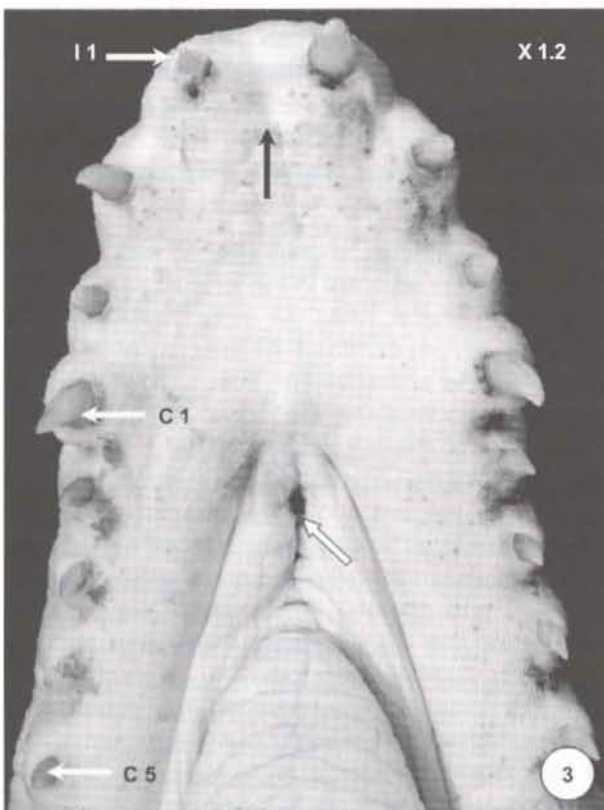


FIG. 3 Macrophotograph of the rostral portion of the mandible (I 1 to C 5). The gingiva is seen to have a slightly cobble appearance towards the rostral tip above the dentary symphysis. The black arrow indicates a shallow depression which houses the small, rigid, conically-shaped maxillary process seen in Fig. 2. The blocked arrow shows a hole made by the hook in the abattoir when the carcass was suspended during the evisceration process. I 1 = Incisor 1; C 1, C 5 = Canine 1 and 5. Formalin-fixed specimen. X 1.2

(Fig. 2) due to the presence of numerous, raised, cobble-like structures. The cobbles on the rostral two-thirds of the palate were large, whereas those occupying the caudo-lateral aspects of the palate were smaller, had a lower profile, but were densely arranged. Between the latter two regions were paired elliptical areas, devoid of cobbles, and which merged medially along the midline of the palate (Fig. 2). These smooth areas corresponded to the positioning of the left and right posterior palatine foraminae which were formed by the caudal edges of the maxillary, the lateral edges of the palatine, a small region of the rostral edge of the pterygoid and

the medial edge of the transpalatine bones. Along the midline of the palate were a series of closely positioned cobbles forming a clearly defined median ridge. This ridge extended from the conical process mentioned above to the base of the dorsal fold of the gular valve. However, the part of the ridge dividing the two smooth elliptical areas above the posterior palatine foraminae was less distinct in nature. The base of the palate adjacent to the dorsal fold of the gular valve displayed a variable number of transverse mucosal folds which closely followed the contours of the dorsal fold across its entire breadth (Fig. 2).

The gingiva of the maxilla was continuous with the palate and could practically be considered to be part of it (Fig. 2). A relatively wide (4–5 mm), clearly demarcated zone of smooth mucosa (possibly representing the palatal aspect of the gingiva) separated the cobbled portion of the palate from the maxillary teeth, from approximately C 3 to M 8. From approximately C 2 rostrally, the surface of the gingiva also had a cobbled appearance similar to that of the palate and the boundary between the latter and the gingiva was not clearly defined. The teeth of the maxilla reflected the dental formula described by Kieser *et al.* (1993) and were carried in the premaxillary and maxillary bones. In the occluded mouth, the teeth of the maxilla were accommodated in grooves to the outside of the mandible, between the teeth of the lower jaw. The tips of the teeth of the mandible were accommodated in pits situated between the teeth of the maxilla, with the exception of C 1, which was accommodated in a maxillary notch and remained visible when the jaws were closed.

The floor of the oral cavity was formed by the tongue and a wide, rostral mucosal plate continuous with the gingiva (Fig. 1 and 3). This plate represented the mucosa-covered surface of the widened rostral tips of the paired dentary bones of the mandible where they met at the dentary symphysis. This plate extended from the rostrally-positioned first two incisors to a point approximately midway between C 1 and C 2 (Fig. 1 and 3). The relatively long tongue was roughly triangular in shape, being much broader caudally than at its tip (Fig. 1). It occupied the greater part of the floor of the oral cavity (apart from the rostral plate over the symphysis of the dentary bones) and was bordered peripherally by a loose, highly folded, continuous, fibrous membrane (Fig. 1 and 3).

The gingiva of the mandible was more clearly defined than that of the maxilla, having a low profiled, cobbled appearance from approximately C 3 rostrally. There was close attachment of the gingiva to the mandibular (dentary and splenial) bones, especially in the region of C 3 (or C 4) to M 7 (or M 8). The rostral tip of the dentary bones formed a broad shelf or plateau (the rostral dentary shelf) which was divided medially by the dentary symphysis. In this region the gingiva had a slightly spongy texture, although the surface also had a cobbled appearance (Fig. 1 and 3). The teeth of the mandible were carried in the paired dentary bones and also reflected the dental formula described by Kieser *et al.* (1993) (see Fig. 1).

From M 4 (or M 5) to M 7 (or M 8) the dentary bone and the medially situated splenial bone were in close association, although the mandibular teeth were clearly housed in the dentary bone.

Light microscopy

The palate

Sections of the palate stained with H&E revealed a keratinised stratified squamous epithelium of variable thickness in all the regions examined. The stratum basale was composed of a single layer of cuboidal to columnar cells resting on a basement membrane. The basement membrane was most obvious in PAS-stained sections and varied in prominence from conspicuous to barely visible. The nuclei of the basal layer of cells were pale, vesicular and round to oval in shape (Fig. 4A). Where oval, the nuclei were oriented vertically to the surface of the epithelium.

The stratum spinosum consisted of 3–6 layers of cells. The cells adjacent to the stratum basale were cuboidal in shape, while the more superficial cells were horizontally flattened. All the cells of this layer displayed the characteristic inter-linking cytoplasmic bridges connecting the individual components. The nuclei of these cells resembled those of the stratum basale. A thin (3–4 layers) stratum granulosum was present above the stratum spinosum. Cells in this layer were spindle shaped or flattened and oriented horizontally. The nuclei were pycnotic, flattened and oriented in the same plane as the cells, while the cytoplasm was filled with strongly basophilic-staining keratohyaline granules (Fig. 4A). The stratum corneum varied in thickness and was composed of a number of compressed layers of cells in which no nuclei were apparent (Fig. 4A). In some areas, particularly towards the gingiva of the teeth and in convoluted regions of the epithelium, a stratum disjunctum consisting of a loose layer of keratinised cells was present (Fig. 4B).

The epithelium was supported by a thick layer of irregular dense connective tissue with prominent bundles of variably oriented collagen fibres being the most prominent feature (Fig. 4A, B, D and E). Sandwiched between the deeper regions of the irregular dense supporting connective tissue and the periosteum of the palatine bones was a well-developed plexus of blood vessels, lymphatics and nerves (medullated and non-medullated). Deeply situated striated muscle bundles were noted only in the region of the posterior palatine foraminae,

stretching from the posterior third of the palate to the base of the dorsal gular fold. No other muscular tissue was observed. Immediately beneath the basement membrane was a thin layer of fine connective tissue which in places displayed a vacuolated, spongy appearance. This region demonstrated a rich capillary blood supply which was intimately associated with the overlying epithelium. No glandular tissue was ever observed in any of the specimens during histological examination of the palate. Lymphocytic aggregations were also not apparent in these sections.

Melanocytes were observed in the connective tissue a short distance beneath the stratum basale, but never within the epithelial layer. The cells were typically dendritic in nature and displayed large numbers of brown to black melanin granules (melanosomes). The melanocytes were concentrated around the capillary plexus beneath the epithelium and also around the larger blood vessels and nerves more deeply positioned within the connective tissue stroma. In some areas the melanocytes formed a diffuse but definite layer beneath the epithelium. The presence of melanin varied amongst individual specimens examined and in some cases it was found to be entirely absent.

Mast cells occurred either singly or in small groups throughout the connective tissue layer with concentrations of five or more cells sometimes being observed. The mast cells were large, round and often observed in the vicinity of blood vessels. The pale, round to oval vesicular nucleus was centrally positioned within the cytoplasmic mass which displayed small fine, evenly distributed basophilic granules. Prominent Pacinian-like corpuscles were randomly scattered throughout the connective tissue layer a short distance beneath the epithelium (Fig. 4B and C). These structures typically consisted of a variable number of connective tissue lamellae surrounding an inner core representing the terminal portion of the innervating nerve. The corpuscle was surrounded by a prominent, dense connective tissue capsule (Fig. 4C) and large medullated nerves were observed in the vicinity of the corpuscles.

Three types of surface specialisations were observed in the sections studied. The first type comprised small pointed elevations of the epithelial lining supported by a core of fine connective tissue (Fig. 4A). In some instances these elevations presented as a series of small localised projections giving the surface of the palate a scalloped appearance. These structures probably represented the epithelial folds

observed by SEM (see below). The remaining two types of specialised structures were characterised by modification of both the epithelium and the underlying connective tissue. Both structures (Fig. 4D and E) displayed a localised thickening of the epithelium due mainly to an increase in the number of layers of the stratum spinosum. The keratinised layer in the region of the epithelial thickening was generally thinner than that of the adjacent tissue. The localised epithelial thickenings were most commonly found in the form of an elevated, dome-shaped structure due primarily to the presence of a diffuse, ellipsoid or conical-shaped mass of loosely arranged connective tissue situated immediately beneath the epithelium (Fig. 4D). These regions were more lightly stained (H&E-stain) than the surrounding connective tissue (due to a reduction in size and number of the collagen bundles) and caused localised protrusion of the overlying epithelium into the mouth cavity. The morphological features of the specialised regions varied. In some instances the diffuse connective tissue core contained a basophilic cell-rich mass situated immediately adjacent to the basal lamina. In other regions, the connective tissue core displayed a paucity of cells, possibly due to the plane of section. Associated with the modified regions of connective tissue were Pacinian-like corpuscles which were either found in or adjacent to this zone. Nerve tissue featured prominently within the modified connective tissue and large medullated nerves and blood vessels were observed entering/leaving at the base of the connective tissue core. The dome-shaped specialisations were distributed throughout the palate but appeared to be more numerous on the rostral aspect up to the rostral border of the posterior palatine foraminae (see Fig. 2).

A small number of localised epithelial thickenings appeared flattened in contrast to the dome-shaped structures and were either positioned level with the adjoining epithelial surface or slightly raised above it. The floor of these epithelial specialisations jutted into the underlying connective tissue layer. Epithelial cells towards the middle of the specialisation adopted a vertical orientation, forming a large elliptical structure reminiscent of a taste bud (Fig. 4E and F). Some of the vertically inclined cells revealed dense, somewhat elongated nuclei, particularly towards the periphery of the elliptical structure, and were similar in appearance to the supporting cells of the mammalian taste-bud. Similarly inclined cells with more vesicular nuclei were seen among the supporting cells and may have represented neuro-epithelial cells. A modified connective tissue

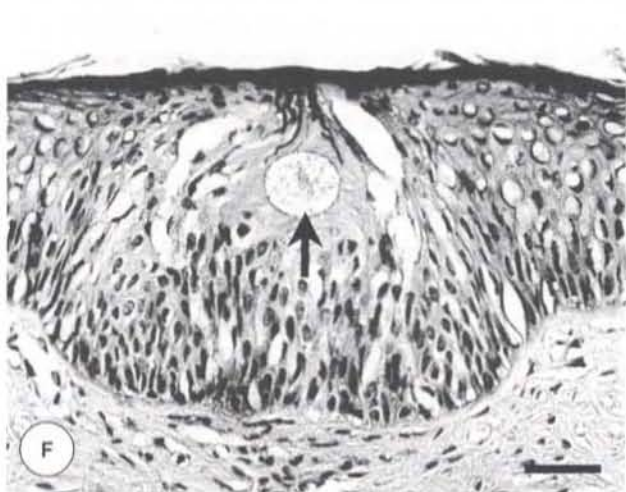
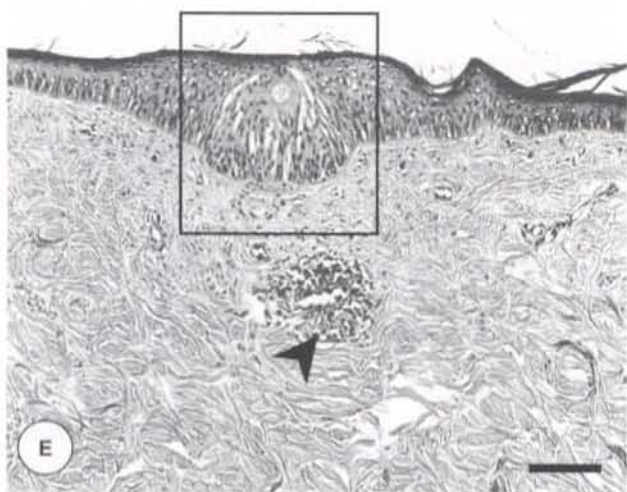
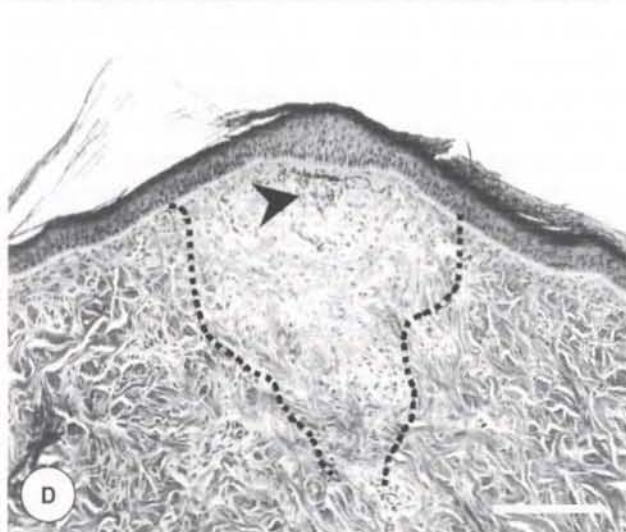
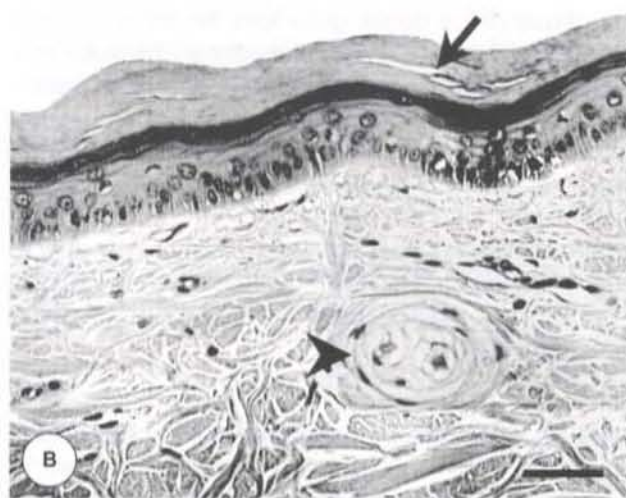
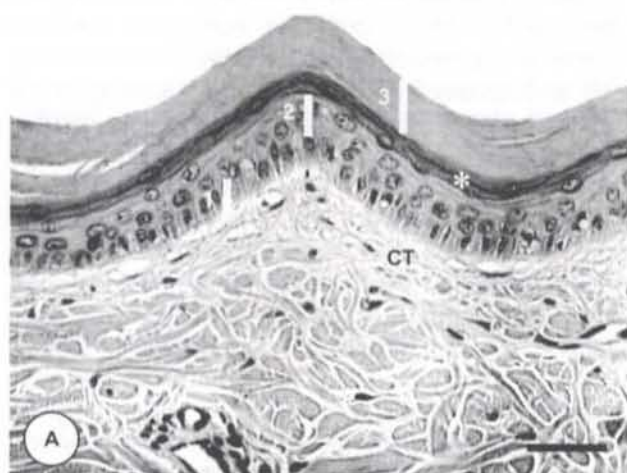


FIG. 4 Histological features of the palate

- A A pointed elevation of the epithelial lining of the palate supported by subepithelial connective tissue (CT). Stratum basale (1); stratum spinosum (2); thin stratum granulosum (asterisk); superficial stratum corneum (3). H&E-stain. Bar = 100 μm
- B Randomly scattered Pacinian-like corpuscles (arrowhead) were located in the subepithelial connective tissue and often associated with epithelial specialisations. Note signs of desquamation of the superficial layers of the stratum corneum (arrow). H&E-stain. Bar = 100 μm
- C Typical Pacinian-like corpuscle displaying concentric lamellae around an inner core (arrowhead). Note the thick, fibrous connective tissue capsule surrounding the corpuscle. H&E-stain. Bar = 50 μm
- D Light micrograph of an elevated, dome-shaped specialisation commonly found in the rostral and lateral regions of the palate showing a pale connective tissue mass (outlined area) below the epithelium. Note the localised thickening of the epithelium and the dark, sub-epithelial cellular mass (arrowhead) H&E-stain. Bar = 500 μm
- E A flattened epithelial specialisation typically found in the mid-, lateral and posterior regions of the palate. Note the dense, dark cellular mass (arrowhead) in the deeper connective tissue associated with these receptors and the arrangement of the epithelial cells to form a structure similar to that of a taste bud (rectangle). H&E-stain. Bar = 250 μm
- F Higher magnification of the epithelial specialisation shown in the rectangle in Fig. 4E. Note the translucent circular structure (arrow) filled with fine fibrillar material. It was not possible to determine the function of this type of corpuscle, but it was thought that they might be associated with taste or osmoreception. H&E-stain. Bar = 100 μm

core similar to that seen beneath the dome-shaped structures was also evident but did not appear to be specifically associated with Pacinian-like corpuscles. Attendant medullated nerves, however, were much in evidence. The taste receptors described above appeared to be concentrated on the more lateral aspects of the palate although they were occasionally encountered towards the midline.

SEM examination confirmed the cobbled appearance of the palate seen macroscopically. It should be noted, however, that individual variation existed in the specimens examined regarding the prominence of the cobbling. Each clearly demarcated cobbled unit displayed a centrally positioned dome-shaped structure or papilla surrounded by an expanse of loosely attached surface epithelial cells. Desquamation of these cells was particularly obvious at the perimeter of the dome-shaped structure (Fig. 5B). In much of the palate (roughly corresponding to the surface in contact with the dorsum of the tongue) the epithelial surface surrounding the papillae was thrown into a number of conspicuous folds which branched and anastomosed (Fig. 5A). The folds displayed a rostro-caudal or slightly oblique alignment. However, towards the periphery of the palate bordering the gingivae and the dorsal fold of the gular valve, as well as in the smooth region of the palate overlaying the posterior palatine foraminae, the cobbled units displayed a featureless surface around the domed papillae.

Some of the domed papillae revealed a small centrally positioned depression and radiating grooves

(Fig. 5C). These structures appeared to occur more commonly in the rostro-lateral regions of the palate. All regions of the palate were characterised by distinct desquamation of the superficial cells of the epithelium. This phenomenon was possibly accentuated by the critical point drying (CPD) process used for SEM sample preparation. Cracking of the epithelial layer was evident in some specimens examined (see Fig. 5C) and was also attributed to the CPD process. Higher magnification of the epithelial surface using SEM imaging revealed the typical polygonal outline of the individual cells, although the borders were not always clearly demarcated. The keratinised surfaces had a coarse, matted appearance (Fig. 5D).

The gingivae

The composition and structure of the gingival mucosa was similar in general appearance to that of the palate, although some variations in structure were apparent. The epithelial surface was more undulating than that of the palate, with occasional elevated structures protruding from the surface (Fig. 6A, C and D). The epithelium itself was thinner than that of the palate, with the stratum corneum and stratum disjunctum forming the most prominent layers. The stratum spinosum was extremely thin and only obvious in regions of localised thickening. Below the basement membrane was a thin layer of vacuolated, spongy connective tissue which was continuous with a thick layer of irregular dense connective tissue.

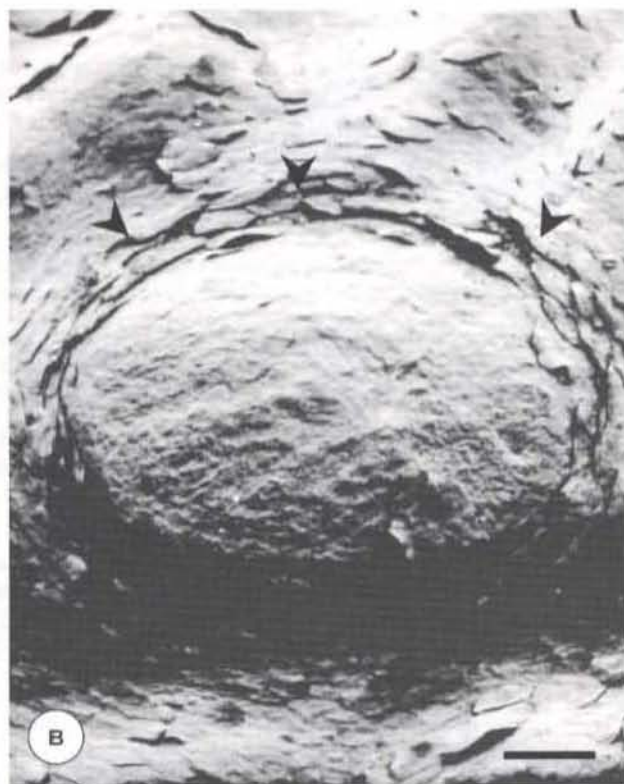


FIG. 5 SEM features of the palate

- A SEM photograph of a polygonal-shaped cobbled unit (arrowheads) typical of the surface of the palate. Note the centrally positioned dome-shaped structure (papilla—circled) and the grooved appearance of the surrounding epithelial surface. Bar = 250 μm
- B Higher magnification of the slightly convex, circular structure circled in Fig. 5A, the surface of which appears featureless. Note the epithelial desquamation (possibly accentuated by SEM processing) around the perimeter of the papilla (arrowheads). Bar = 50 μm
- C A convexly raised papilla with a central depression (asterisk) with radiating grooves (black arrowheads). These papillae were observed in the rostro-lateral regions of the palate. Light desquamation is also apparent (white arrowheads). The block arrows indicate artefacts (cracking of epithelium) probably caused during SEM processing (critical point drying). Bar = 100 μm
- D Higher magnification of the typical cell-surface features seen throughout the palate. The arrows indicate the boundaries of a characteristic polygonal-shaped cell. Note the complex pattern of microridges on the cell surface. Bar = 2 μm

The occurrence, appearance and organisation of mast cells, melanocytes, vascular and nerve plexuses was similar to that seen in the palate. Surface specialisations similar to those seen in the palate were evident in the gingiva, namely, the small, pointed epithelial elevations and the larger specialised structures displaying modification of the epithelium and the underlying connective tissue. These structures were particularly obvious at the rostral aspect of the mandible although they were found throughout the gingivae. The small epithelial projections probably represent the conical processes seen by SEM (see Fig. 6D). The raised, dome-shaped structures with a thickened epithelium were, as in the palate, associated with Pacinian-like corpuscles situated in the vicinity of the modified connective tissue core. However, the Pacinian-like corpuscles appeared to be more abundant in the gingivae, with three to four sometimes being associated with each specialisation. The thickened, non-elevated epithelial specialisations typically also displayed structures resembling taste buds. The "taste bud" was generally situated in the centre of the thickened epithelial lining, although pairs of "taste buds" were sometimes observed (Fig. 6B and E).

SEM of the gingiva revealed a series of raised, dome-shaped structures each of which was surrounded by two concentric rows of smaller, raised conical projections (Fig. 6D). These structural units appeared most concentrated on the shelf above the dentary symphysis (rostral dentary shelf) of the mandible and showed smaller concentrations at the base of each tooth (see Fig. 6C), from I 1 to C 5, but progressively reduced in numbers caudally on the lingual surfaces of the dentary and splenial bones. The gingiva of the maxilla also displayed a

reduced number of these structural units. Situated between some of these units were small, flattened and slightly depressed, circular areas, often displaying a centrally situated pore (Fig. 6D). Pairs of closely associated pores were also occasionally seen (Fig. 6E). Higher magnification of the flattened discs sometimes showed a mass of fimbriae protruding from the pore (Fig. 6E and F). The pores are believed to represent the opening on the surface of the underlying "taste buds" and were sometimes difficult to observe by SEM due to occlusion of the pore by cellular debris. The flattened areas did not occur constantly between the domed units described above and also did not appear to be arranged in any sequence or pattern, but their occurrence was most common on the rostral dentary shelf. On occasion they also occurred isolated from any other epithelial specialisations, although they displayed similar morphological features.

Desquamation of the surface cells was much in evidence and the surface features of the cells were similar to those seen in the palate (see Fig. 5D).

Examination of fresh specimens from the palate and gingiva showed that the cobbled units described above did not display epithelial folding as prominently as formalin-fixed or critical point dried specimens. This phenomenon was presumed to be associated with the shrinking effect of fixation and the processing of the tissue samples for SEM observation.

DISCUSSION

Meaningful gross morphological descriptions of the oral cavity of the Crocodylia are not available in the literature and it appears that only specific speciali-

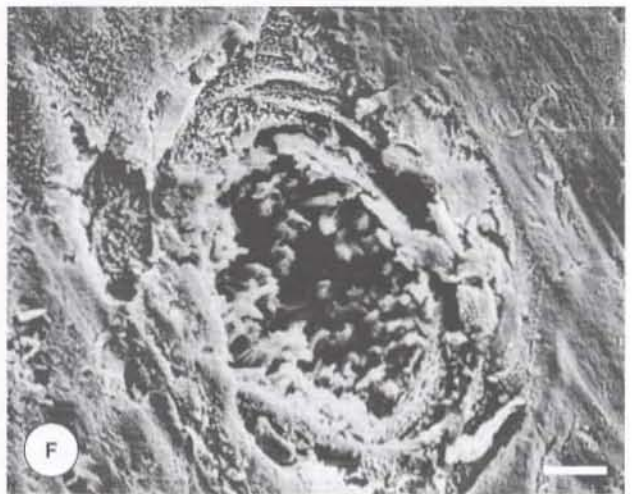
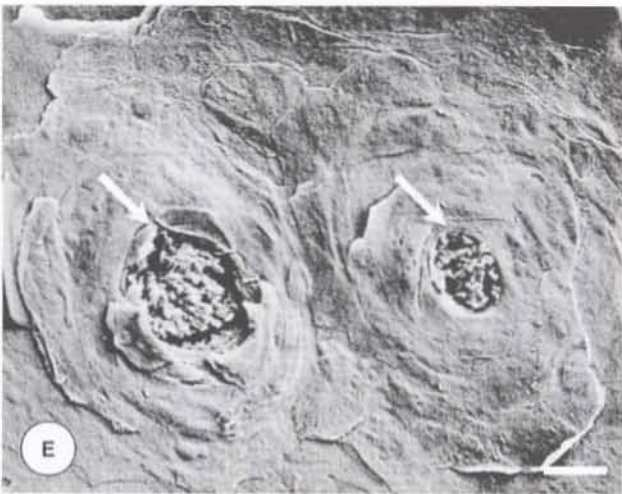
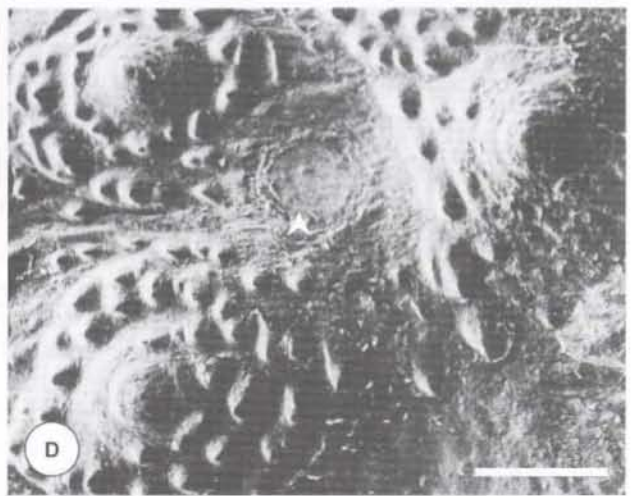
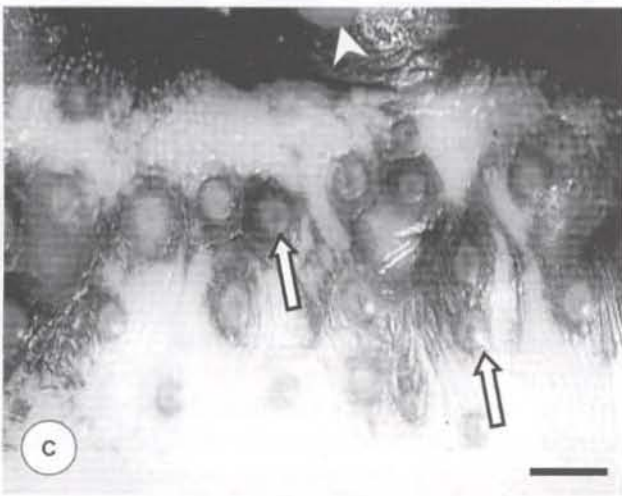
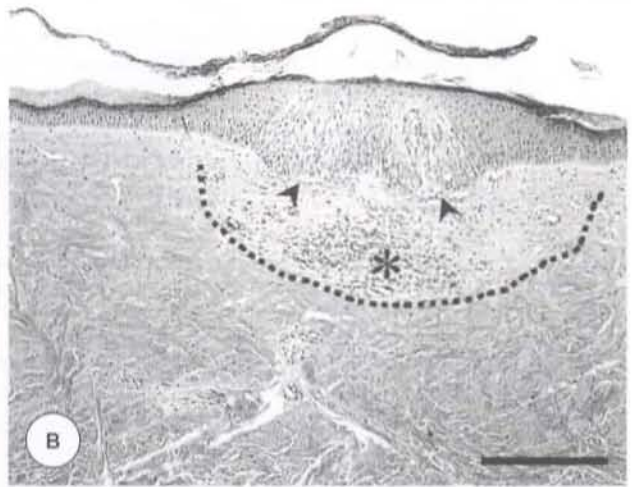
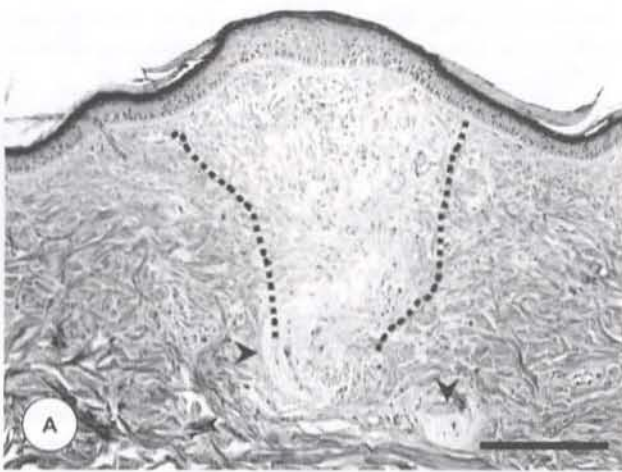


FIG. 6 Morphological features of the gingivae

- A Light micrograph of a raised sensory unit commonly found in the rostral region of the mandible showing a pale connective tissue mass (outlined area) below the epithelium. Two Pacinian-like corpuscles (arrowheads) are closely associated with the base of the modified region of connective tissue. H&E stain. Bar = 500 μm
- B Light micrograph of paired structures (arrowheads) resembling taste buds within a flattened epithelial specialisation. This type of specialisation was generally found in the rostral and mid-lateral gingivae of the mandible. Note the pale connective tissue mass (outlined area) similar to that shown in Fig. 6A below the specialisation. A diffuse, basophilic cell-rich mass (asterisk) is observed within the connective tissue. H&E stain. Bar = 500 μm
- C Stereomicrograph of epithelial specialisations (arrows) in the rostral region of the gingiva of the mandible. The specialisations were normally situated close to teeth (white arrowhead). Fresh specimen. Bar = 500 μm
- D SEM photograph of a group of epithelial specialisations, similarly situated to those shown in Fig. 6C. Each dome-shaped papilla (shown in sagittal section in Fig. 6A) is in turn surrounded by rosettes of conical epithelial projections. Note the flattened circular area (arrowhead) in the centre of the group of papillae, indicating the flattened type of epithelial specialisation seen in sagittal section in Fig. 6B. Bar = 500 μm
- E SEM photograph of paired pores (arrows) associated with the taste buds contained within flattened epithelial specialisations similar to those shown in Fig. 6B and 6D. Bar = 10 μm
- F Higher magnification SEM photograph of one of the sensory pores seen in Fig. 6E showing exposed fimbriae. Bar = 5 μm

sations and structures (glands, dentition, the development and structure of the palate and osteology) have been described. Although illustrated in a number of papers, the cobbled appearance of the epithelium of the palate and parts of the gingivae have not drawn any comment by the authors. Certainly, the small, rigid, conically shaped process (Fig. 2) which emerged from a low-profiled ridge above the anterior palatine foramen has not been described. The true structure and function of this process is unknown and was not specifically examined in this study, but may well prove an interesting topic for further investigation. Similarly, the description of the clearly defined median ridge, comprising a series of closely positioned cobbles along the midline of the palate, appears also to have drawn no attention from previous authors. The presence of a broad dentary shelf forming the rostral aspect of the mandible (see Fig. 1A and 3), and which is richly supplied with sensory structures, is likewise not specifically mentioned in the literature.

In his generalised description of the reptilian oral cavity, Luppá (1977) noted that within the oral cavity of the Reptilia, the epithelium showed considerable regional and specific variation and that within a single species, compound squamous epithelium, ciliated epithelium, goblet cells and simple non-ciliated columnar epithelium may be found. This study revealed that the epithelium of the oral cavity (including the surface of the tongue) varied little in structure except for the lining of the oral aspect of the dorsal and ventral folds of the gular valve.

Throughout the oral cavity the epithelium was a lightly keratinised stratified squamous epithelium which showed slight localised variation in thickness.

A relatively thin stratified squamous epithelium lined all aspects of the palate. However, towards the base of the dorsal fold and on the oral surface of the ventral fold of the gular valve, there was a sharp transition from the lightly keratinised epithelium to a thick, non-keratinised stratified squamous epithelium with prominent epithelial and connective tissue papillae (personal observation). Throughout the palate, the epithelium was supported by a thick layer of irregular dense connective tissue at the base of which, adjacent to the periosteum of the palatal bones, were well-developed plexuses of blood vessels, lymphatic vessels and nerves. Adjacent to the basement membrane was a layer of melanocytes. Variation in density was apparent amongst specimens examined and in some cases no melanin appeared to be present. This region is similarly described by Taguchi (1920) who also mentions a scattered presence of "pigmented cells", presumably melanin containing cells.

The general composition of the epithelium of the gingivae appeared very similar to that of the palate, although the gingivae had a more undulating surface. The epithelium itself was slightly thinner than that of the palate, with the stratum corneum and stratum disjunctum forming the most prominent layers, particularly in the immediate vicinity of the teeth.

The occurrence of glands and the presence of taste receptors (sensory neuro-epithelial cells, [Luppa 1977] or "Schmeckzellen" of Krause [1922, cited by Luppa 1977]) appear to dominate descriptions amongst authors who have examined the histology or morphology of the oral cavity of crocodiles. Kochva (1978) extensively describes glandular tissue in reptiles, but only fleetingly refers to the Crocodylia (*Caiman* spp., *A. mississippiensis* and *C. niloticus*) noting only that "A cursory examination of some slides of *Crocodylus niloticus* reveals no sublingual glands". In an earlier study Woerdeman (1920) observed that the oral cavity of reptiles was highly glandular, but that crocodiles appeared to be an exception and that various authors had reported the absence of glandular tissue. Woerdeman (1920) also reviewed earlier literature (ca. 1888 to 1914) on the subject and emphasised discrepancies amongst the authors regarding the presence or absence of oral glands in Crocodylia. Gaupp (1888, cited by Woerdeman 1920) described the presence of small *Glandulae linguales* but concluded that *Glandulae sublinguales* and *Glandulae palatinae* were absent. Stannius (no reference, cited by Woerdeman 1920) stated that crocodiles did not have any salivary glands. Gegenbaur (1901, cited by Woerdeman 1920) reported the absence of labial glands in crocodiles. Schimkewitsch (1910, cited by Woerdeman 1920) however, describes medial and lateral glandular groups in the palate of crocodiles. These *Glandulae palatinae*, according to Schimkewitsch (1910), were the equivalent of the intermaxillary glands in amphibians.

Farenholz (1937) reported two areas in the palate in which glands occur, *viz.*, median palatine glands, found only in *Caiman* and small glands at the median aspect of the maxillary teeth, found in *Caiman* spp. and *A. mississippiensis*. Woerdeman (1920), while investigating tooth development of *Crocodylus*, found that the development of glands, previously described by Röse (1893), was closely associated with the development of the dental system. These glands were observed to open into pits situated between the maxillary teeth and into which fit the tips of the mandibular teeth. The glands are medially situated in the pits and are surrounded by soft connective tissue and covered by a stratified squamous epithelium. The region between the maxillary teeth (i.e., the pits into which the tips of the mandibular teeth fit) was not examined during this study and it is thus not possible to comment on the presence or absence of any glandular tissue in this region. However, Taguchi (1920) found glandular

tissue "in the submucosa of the caudal part of the palate and the oral surface of the velum" in all three species he examined and described the glands as being branched tubulo-alveolar mucous glands. This statement indicates that Taguchi found two clear zones of glands, albeit in close proximity to each other. This investigation clearly indicated that there was no glandular tissue in the palate "proper" and that glandular tissue (as described by Taguchi 1920) only occurred on the oral surface of the dorsal fold of the gular valve (personal observation).

Although dentition was only superficially examined in the Nile crocodile during this study, it became important when sampling methods of the palate and gingivae of the lower and upper jaws were considered. Teeth were therefore named and numbered according to Kieser *et al.* (1993), who concluded that the Nile crocodile was heterodont and had five premaxillary incisor, five canine and six or more post canine (molar) teeth in the maxilla. The dental arrangement in the mandible was three pre-mandibular incisor, five canine and six or more post canine (molar) teeth. The teeth of the mandible were accommodated in the paired dentary bones which united at the rostral, elongated dentary symphysis (see Lordansky 1973 for osteology of the crocodylian skull). Each tooth emerged from its own alveolus in the dentary bone. The caudal region of the splenial bone, situated medially to the dentary bone, was in close association to molar teeth M 4 to M 7 (or M 8), but did not form part of the accommodation of the teeth in the jaw. This is in contrast to the findings of Chiasson (1962) who examined the alligator and stated that the dentary bone "bears the first 14–15 teeth in individual alveoli on each side, the remaining 5–6 teeth being held in a common groove between the dentary and splenial bones." The teeth of the maxilla were similarly accommodated in individual alveoli in the premaxilla and maxillary bones, which also formed the major portion of the palate. Chiasson (1962) stated that in the alligator there were "15 to 16 maxillary teeth on each side. The first few of these are held in individual alveolar sockets but the posterior series are set side by side in a common groove."

Pressure receptors are noted by Pooley & Gans (1976) to occur "between the teeth and (in) the jaws" of the Nile crocodile and that they function to gauge the intensity of a bite. They do not, however, give any histological description of these receptors, but do state that similar receptors are found in mammals, including humans. This investigation revealed that lamellated, Pacinian-like corpuscles were fre-

quently observed in the palate and the gingivae (see Fig. 4B, C and 6A). These corpuscles were often associated with dome-shaped epithelial specialisations, the latter structures appearing more numerous in the lateral and rostral regions of the palate and in the gingiva covering the rostral dentary shelf (Fig. 1 and 3). Similar raised structures have been described by Von Düring (1973, 1974) on the cranial scales of *Caiman crocodilus*. These cranial touch papillae or integumentary touch papillae are also associated with structures resembling mammalian Pacinian corpuscles and the illustrations presented in the papers of Andres & Von Düring (1973), Von Düring (1973) and Von Düring & Miller (1979) reveal lamellated structures similar to those observed in the oral cavity of *C. niloticus* in the present study. In contrast, Jackson, Butler & Youson (1996) described slightly convex integumentary sense organs (ISOs), which only occur on postcranial scales of crocodylids and gavialids and which are not associated with Pacinian-like corpuscles. Despite the absence of the Pacinian-type corpuscles, the micrographs (LM and SEM) and illustrations presented by Jackson *et al.* (1996) of the ISOs reveal certain similarities to the dome-shaped structures described in the present study, namely, the domed, low profiled elevation of the epithelial component of both structures and the underlying pale-staining zone of connective tissue (H&E-stain). Jackson *et al.* (1996) refer to the modified connective tissue component of the ISOs as a "diffuse pocket in the dermis" and that it contains fluid. They further note that this diffuse pocket contains very few collagen fibres in comparison to the surrounding connective tissue, an observation also made in the oral cavity in this study. Based on their structural characteristics, Von Düring (1973, 1974) described the touch papillae as being mechanosensory in nature. Conclusions drawn by Jackson *et al.* (1996) were that the ISOs identified by them possibly had a mechanosensory or chemosensory function and that further physiological studies would have to be performed to determine their true function. Based on these comments it would appear that the dome-shaped structures associated with Pacinian-like corpuscles found in the oral cavity of the Nile crocodile function as pressure receptors.

Hulanicka (1913) examined the nerve endings in the tongue, palate and the skin of two species of crocodile, *viz.*, *C. niloticus* (eight young specimens examined, 25–45 cm in length) and *A. mississippiensis* (three young specimens examined, 65–110 cm in length) and described five types of nerve endings in the tongue, palate and the abdominal

skin. These were free nerve endings (in the palate), touch cells (in the stroma of the tongue, dermis of the skin, stroma of the stomach, chin and jaws), tactile papillae (in the skin and in the mucosa of the tongue and palate), tactile corpuscles (in the stroma of the tongue, the palate and in the dermis of the skin) and taste buds as described by Bath (1905, 1906). Hulanicka (1913) described two types of tactile papillae in the mucosa of the palate; the first type was small and pointed and covered by a relatively thin epithelial layer, while the second type was much larger, rounded at the tip and covered by a thicker epithelial layer than that of the pointed papillae. This description corresponds broadly with the pointed (conical) processes and the dome-shaped structures respectively, identified in the present study. The tactile corpuscles identified and illustrated by Hulanicka (1913), however, bear little resemblance to the Pacinian-like corpuscles observed in our specimens. Hulanicka (1913) does note that the size and distribution of the sensory structures change with the age of the specimen. To what extent the larger (older) crocodiles examined in this study (compared to the relatively small specimens described by Hulanicka) reflect age related differences, could not be determined. Although the specific innervation of the oral cavity was not examined during this study, it was found, as described above, that the palate and gingivae were rich in Pacinian-type corpuscles.

It is of interest to note that the diagrammatic representation of sensory nerve endings and the distribution of nerves in tactile papillae in the palate of *A. mississippiensis* presented by Hulanicka (1913), correspond to the general form of the light-staining connective tissue cores underlying the sensory epithelial structures seen in micrographs presented in this study (see Fig. 4D and 6A, B).

Luppa (1977), who generalised his description of the histological composition of the reptilian oral cavity, reported that taste buds were scattered throughout the epithelium of the oral cavity in reptiles and that in *Lacerta* the taste buds were most numerous laterally and on the palatal folds. Luppa (1977) further reported that reptilian taste buds showed no significant differences in their cellular composition from those of mammals and that sensory neuro-epithelial cells (= Schmeckzellen of Krause 1922, cited by Luppa 1977) and supportive cells occurred in both mammals and reptilians. Bath (1905, 1906) studied the structure as well as the distribution of taste receptors in the Nile crocodile and the alligator, and reported taste receptors

towards the back of the oral cavity and in the pharyngeal cavity and upper region of the oesophagus of *C. niloticus*. Taguchi (1920) identified small numbers of taste buds in the palate of *C. niloticus* and *C. porosus* but not in *A. sinensis*. Sensory structures observed during this study in the epithelium of the palate and gingivae, and presumed to be taste buds, were of similar morphology to those described by Bath (1905, 1906) and Taguchi (1920). Hulanicka (1913), however, disputed some of the findings of Bath (1905, 1906) regarding the structure of taste receptors in the species he examined, specifically the association between support cells and the nerve fibres innervating the taste bud. In this study the taste buds displayed typical longitudinally oriented supportive and neuro-epithelial cells and were observed to be associated with medullated nerve concentrations situated in the connective tissue at the base of the taste receptors. In addition, this study graphically illustrated by SEM the cuticular processes of the neuro-epithelial cells where they emerged through the taste pore (see Fig. 6E and F).

Although they occurred throughout the palate and gingivae, taste receptors were less common than the ubiquitous pressure receptors. However, the presence of both types of sensory receptors in the palate and gingivae points to the important functional role played by both components of the oral cavity in monitoring taste and pressure.

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